COMMUNITY PRESERVATION IN RECENT SHELL-GRAVELS, ENGLISH CHANNEL

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ABSTRACT. Live and dead benthic faunas have been sampled offshore from Plymouth to assess the relationship between dead shell accumulations and living benthic communities. The live fauna (354 samples) has been sampled at approximately twenty-year intervals since 1895. The dead fauna (25 samples) was collected in one survey in 1980-1981. The live and dead mollusc and echinoderm (185 taxa) abundances are compared using multivariate statistical analysis (Detrended Correspondence Analysis).

Three distinct communities are defined by this analysis, inhabiting shell-gravel, sand, and mud substrates. Historic records of the shell-gravel community indicate population fluctuations, and present-day faunas are most similar to those recorded in the 1920s. The dead shell-gravel fauna is similar to the 'time-averaged' live fauna and distinct from the sand and mud communities. When bivalves alone are analysed then relative abundances are preserved in dead samples even though these show greater abundance, diversity, homogeneity, and equitability. The results give support to the interpretation of original time-averaged community structure from similar fossil shell beds. However, fluctuations in population structure are not preserved because of the slow sedimentation rates.

ONE of the fundamental, but still unsolved, problems in palaeocology concerns the nature of the relationship between preserved fossil assemblages and their original benthic communities. Most authors consider that the best way to study this relationship has been the investigation of live communities and their accumulating preservable remains. Many papers have been published during the last twenty years using this approach. The majority of workers obtained their data from a single sampling programme of both live and dead shelly faunas. The difficulties of sampling offshore soft-bottoms have probably contributed to the concentration of many studies from inshore regions. Thus Peterson (1976) and Warme (1969) studied shallow lagoons off the Californian coast; Johnson (1965), Cadée (1968), Evans (1968), McCall and Tevesz (1983) studied enclosed bays or estuaries; Van Straaten (1960), Habe (1956), MacDonald (1969a, b), Wilson (1967), and Antia (1977) investigated inter-tidal flats; Bosence (1979a, b) studied a shallow open-bay environment. The geologically important shelf environment has not received so much attention and only Hertweck (1972) and Wilson (1982) have ventured into deeper shelf waters.

The consensus of this research is that there is a general correspondence between the communities and death assemblages but that the structure of the original community is lost because of a number of processes operating on the accumulating dead material. Post-mortem transportation is emphasized by Cadée (1968), Bosence (1979a, b), Wilson (1982), and Farrow et al. (1984). Post-mortem dissolution is considered important by Peterson (1976) and McCall and Tevesz (1983), but these authors were probably dealing with undersaturated sea water; it has not been considered important in open marine waters supersaturated with respect to calcium carbonate (Alexandersson 1979; Bosence 1979a; Wilson 1982). Fragmentation during predation can also effect the taxonomic composition of the dead assemblage (Cadée 1968; Bishop 1975; Farrow and Clokie 1979). Changing environments and local habitats also cause important differences between the results of surveys of live and dead material (Bosence 1979a; Powell et al. 1982). The latter authors stress the importance of this in establishing community composition prior to present-day sampling. The major sources of differences between Recent live and dead populations is, however, the short-term fluctuations and patchy distributions characteristic of live benthic communities (McCall and Tevesz 1983). Because of the high variability of Recent communities, a single sampling will, at its best, only represent the
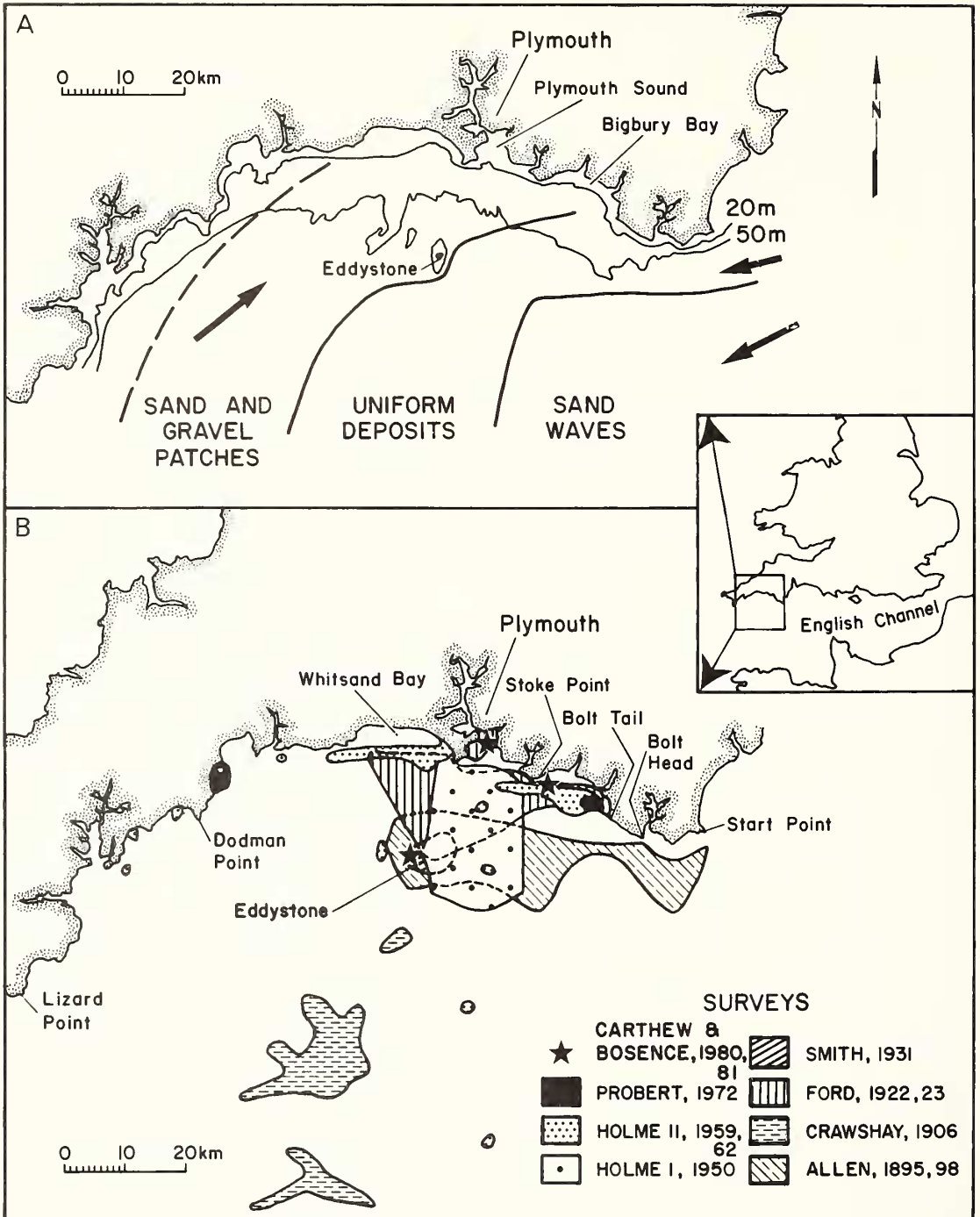
TEXT-FIG. 1. A, sea floor topography, substrate composition below 20 m, and direction of sand transport (arrows); redrawn from Fleming and Stride (1967). B, localities and dates of the surveys (not publications) in the western English Channel. Where the surveys overlap, the more recent survey overlies the older.

nature of that community at that instant of time. The occurrences of individual taxa will depend on such factors as the last successful spatfall, local predation levels, the successional state of the community following local disturbance, and other biotic interactions or changes in the substrate. Such short-term fluctuations in soft substrate communities have been reviewed by Gray (1977) who concludes that the community has an internal stability or resilience whereby temporarily disturbed communities will return to an earlier organization if the perturbation is removed. Gray (1977) quotes several cases of temporary dominance changes following perturbations.

Because of the fluctuations in live communities, accumulating death assemblages have been referred to as 'time-averaged' by Walker and Bambach (1971). The dead material accumulating over a period of time can be considered to average these short-term fluctuations in live populutions. This aspect of community preservation is also discussed by Warme *et al.* (1976) and Fürsich (1978) who also introduces the term 'faunal-condensation' which occurs when sedimentation rates are slow compared with community production rates. One result of time-averaging and faunal condensation is that it is most unlikely that short-term variations such as ecological succession (autogenic) or the effects of predator–prey fluctuations will be preserved in soft-bottom substrates (McCall and Tevesz 1983; Paine 1983). McCall and Tevesz (1983) suggest that the preservation of succession is most unlikely with average shelf sedimentation rates and from a critical review of the literature suggest that only two examples are known to date. These are the studies described by Walker and Parker (1976) and Johnson (1977).

Another major effect of these fluctuations is that we should not expect to find a good correspondence between the results of one sampling programme of the living community and the associated accumulating death assemblage. Correspondence could only be expected with relatively stable communities and high sedimentation rates. In most geological examples the fossil assemblage might be expected to be more similar to the long-term (tens or hundreds of years) community composition.

This paper presents the results of a comparison of long-term, live faunal sampling with the present-day death assemblage from an offshore environment (text-fig. 1A). The benthic communities of the English Channel have been studied by scientists from the Marine Biological Association's Plymouth Laboratory at various periods over nearly one hundred years. The results of these surveys present a unique opportunity to investigate the longer-term community structure and its relationship to the accumulating death assemblage.

Systematic sampling of the benthic communities of the western Channel was started in the 1890s by Allen (1899) who covered grounds extending from the Eddystone to Start Point (text-figs. 1B, 2A). Crawshay (1912) sampled a strip south of the Eddystone to the centre of the Channel. Ford (1923) extended Petersen's (1914) classic study on benthic communities from the Danish waters to the English Channel. He included the Plymouth Sound and Eddystone shell-gravels together with other areas to the south of Plymouth (text-figs. 1B, 2A, B). Smith (1932) carried out a detailed survey of the Eddystone shell-gravels. Holme (1953, 1961, 1966) has carried out extensive surveys of the fauna of the western Channel which also include the Eddystone shell-gravels. Finally, Probert (1973) sampled areas mainly to the west of Plymouth but included Bigbury Bay, an area previously sampled by Ford (1923). Therefore, the previous work (summarized in text-fig. 1B) covers four previous samplings of the shell-gravels around Eddystone and one from the Plymouth Sound shell-gravels. Sampling to update these records for this project was carried out during September 1980 to May 1981 and included the live fauna together with the dead fauna of three shell-gravel sites: The Eddystone, Plymouth Sound, and Stoke Point (text-fig. 2). The previous surveys of the surrounding, mainly finer-grained sea bed provides a useful comparison and have all been included in the analysis. The total data come from some 379 samples, the majority of which were investigated by many replicate samples. A multivariate analytical technique was used to study the variation within these data, to compare live and dead faunas within surveys, and to compare the present-day dead fauna with previous live surveys and previous surveys of the live fauna with each other.
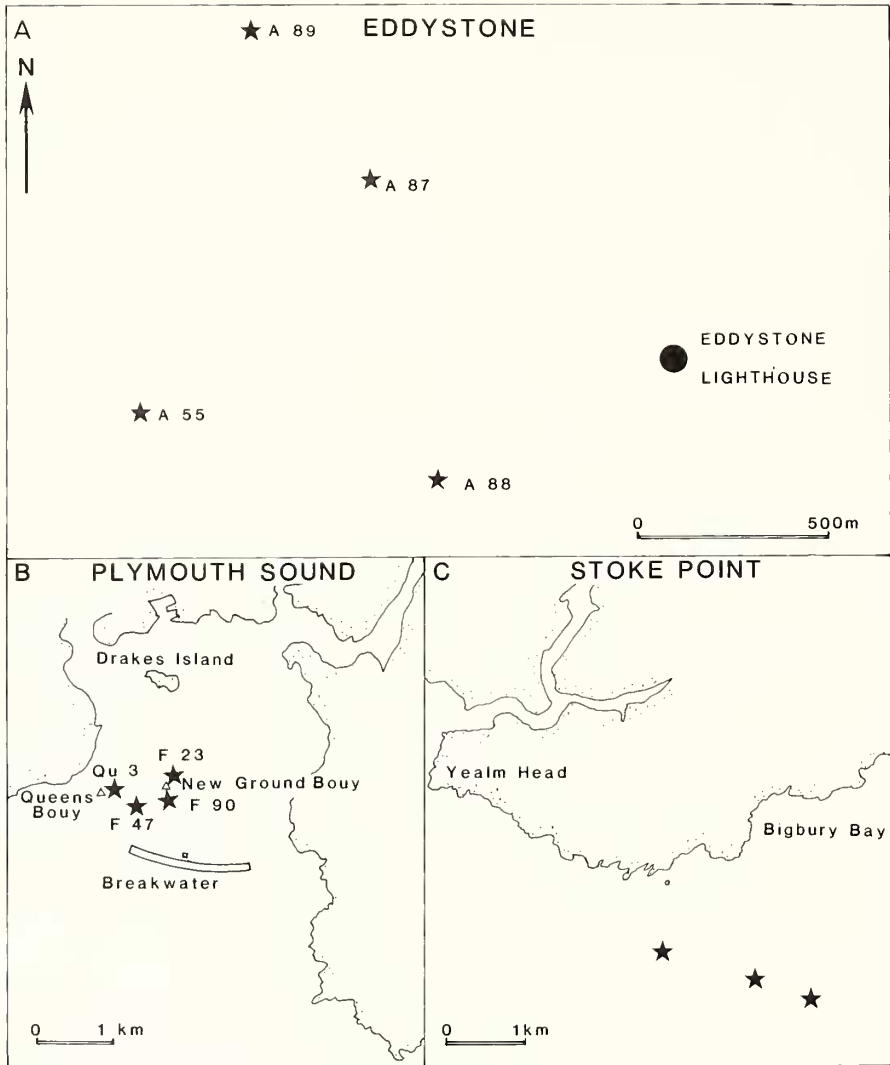
TEXT-FIG. 2. Locations of sample stations of earlier workers and those sampled for this study. A, Eddystone. B, Plymouth Sound. C, Stoke Point. (See Appendix 2 for details of sample positions.)

THE SHELL-GRAVELS AND THEIR FAUNA

Shell-gravels

Unfortunately there has been little detailed sedimentological work undertaken in the Plymouth–Eddystone area. Apart from the qualitative and some quantitative (Holme 1953) descriptions in the biological surveys, the only account of these sediments is by Fleming and Stride (1967).

The Recent sediments comprise sand and gravel patches to the west and a sand sheet to the east (text-fig. 1A). The sediments are deposited on either the rock floor, as at Eddystone, or on a terrigenous conglomerate presumed to be a deposit of the post-glacial transgression. Sand patches are up to 10 cm thick and formed of well-sorted medium- to coarse-grained terrigenous sand. They

are rippled by tidal currents and can be seen to overlie the gravel patches. Gravel patches are composed of a fine gravel (median diameter 2·6 mm), dominantly of terrigenous origin. Shell sand may, however, make up 40% of the fine sand grade. Gravel patches are rippled by winter storms and are up to 25 cm thick. The sand sheet to the east (text-fig. 1A) is being transported westwards and is composed of a fine sand. Sand waves are found to the south of Bolt Head which pass westwards into 'uniform deposits' towards Eddystone (Fleming and Stride 1967). Boillot (1965) describes the terrigenous and bioclastic sediments south of this area.

The shell-gravels of this study occur within the sand and gravel patches. The Eddystone gravels occur around 60 m deep rock outcrops which extend to the surface at Eddystone Rocks. Smith (1932) records three types of gravel arranged concentrically around the Rocks. The 'inner gravel' is characterized by locally derived gneiss pebbles and shell debris. The 'middle gravel' contains little terrigenous material and is rich in broken and unbroken shells. The 'outer gravel' contains sandstone pebbles and broken shells. In general, the grain sizes of both the total and the shelly component decrease away from the rocks. Our samples (text-fig. 2) are from the inner and outer shell-gravels (60–64 m) at stations previously sampled by Allen (1899) and Smith (1932). The shell-gravels of Plymouth Sound at Queens and New Ground (Ford 1923) and occur at depths of 13–16 m. The Stoke Point gravels occur off a rocky shore at intermediate depths of between 32 and 43 m (text-fig. 2; Appendix II).

Although the processes leading to shell-gravel formation at these three sites are not understood, they are all affected by strong currents generated by south-westerly storms. Even though the Plymouth Sound stations are in an enclosed area they are open to the south-west. The Eddystone gravels would be expected to experience higher currents than surrounding sandy areas of the sea-floor because of shallowing and wave refraction. Data in Draper (1967) and Channon and Hamilton (1976) suggests that medium sand-sized quartz sediment could be expected to be transported on nearly 100 days during the year at depths of 60 m in the western Channel. In the absence of further information, it seems likely that the gravels occur in sites of low terrigenous supply and/or winnowing of finer-grained sediment.

Wilson (1982) proposes a model for shell-gravel formation which, with the presently limited information available, can be applied to the shell-gravels discussed here. He suggests that with transgression and limited terrigenous sediment supply, sands are swept into patches or sheets over the basal conglomerate. With no further terrigenous supply carbonate grains are generated from epifauna on exposed boulders and rock outcrops and the sand sheets are only added to by infaunal production from the sands. With time, biogenic production increases the grain size of the sand to a shelly-gravel. The shelly-gravels as they coarsen become less favourable to burrowing by their original fauna and they are replaced by those taxa which tolerate the coarser sediments. In addition, production from nearby rocky outcrops may contribute carbonate grains. Periods of increased current strength would tend to winnow out the smaller clastic grains thus contributing to the increase in grain size. The increased grain size will also make the gravels more resistant to erosion and the largest grains may in turn support their own calcareous epifauna.

Fauna

The shell-gravels have a characteristic fauna which is dominated by robust-shelled suspension feeding bivalves: *Venus fasciata*, *V. ovata*, *V. casina*, *Glycymeris glycymeris*, *Venerupis rhomboides*, *Gouldia minima*, *Arcopagia crassa*, *Tellina pygmea*, *Gari tellinella*, and *Spisula solida*. Smaller common bivalves are *Astarte triangularis* (living within the gravel interstices), *Montacuta ferruginose* (symbiotic with *Spatangus purpuratus*), and the deposit feeding *Nucula hanleyi*. The infaunal echinoids *Spatangus purpuratus* and *Echinocyamus pusillus* are also common as are the polychaetes *Polygordius lacteus* and *Glycera lapidum*. Other characteristic but soft-bodied organisms are the infaunal cephalochordate *Amphioxus lanceolatus* and the amphipod *Ampeliscina typica*. Therefore the community has a very high proportion of preservable taxa. The taxa considered in this paper from the analyses of past and present surveys are the macrofauna from the Bivalvia, Gastropoda, and Echinodermata.

METHODS

Sampling

Most authors used different sampling techniques (Table 1) which has resulted in variable quality of data for analysis of the historic faunal records. Ford (1923) and Holme (1953) used grabs which, while producing reasonably quantitative data on fine substrates, have problems caused by incomplete closure and 'washing through' in coarse shell-gravels. In addition, with sparsely distributed or patchy faunas many samples are required to obtain representative numbers of even the commonest taxa. The two authors used grabs of different design which would be expected to behave differently on similar substrates (see discussion in Holme and McIntyre 1984). Other workers used dredges (Table 1) which, while being easier and quicker to operate, may cover a large and unknown area of the sea bed. Some dredges (i.e. Anchor and Modified Naturalist's) bite into the sea bed whilst others (Naturalist's) as well as Otter and Beam Trawls do not bite so deep and may travel some distance over the sea bed sampling different populations. For this survey, sampling was carried out from the Marine Biological Association, Plymouth, using small vessels and a Naturalist's dredge modified with a curved metal frame allowing it to bite into the sea bed. At each station (sampled at slack water) the dredge was dropped with 2–3 times the warp required for known water depth. The boat was moved gently until the warp was taut and following a few rapid turns of the engine the dredge was fast on the sea bed. After retrieval the boat returned to the station for a replicate haul in the same direction. Initially a 10 l sample was taken from the centre of the 2 mm dredge bag and the live and dead fauna counted. Because of the time involved in sorting and counting the faunas (some taxa occur over a thousand times in one sample) subsamples were taken. No new species were being recruited after 3 l of sediment for the live fauna and 2 l of sediment for the dead fauna and these volumes of sediment were therefore chosen for sorting. The counts of occurrences of individuals and species per sample for our stations and those of previous authors are obtainable as computer listings deposited with the British Library, Boston Spa, Yorkshire, UK, Supplementary Publication No. SUP14026. The data matrix comprises a total of 185 taxa occurring at 379 samples. A species occurrence list and species authors' are given in Appendix 1.

The live fauna was surveyed in November 1980 and in January, March, and May 1981 to compare seasonal variations. At least two replicate samplings of the dead fauna were taken from each station.

Four of Allen's (1899) stations were relocated on the south-west British Chain Decca from Allen's bearings (corrected for magnetic deviation) and distances from the Eddystone Light (Appendix 2). Four of Ford's (1923) stations were relocated using Ford's transits or sightings (Appendix 2) and three new stations of shell-gravel from Stoke Point were sampled. Allen's (1899) samples are, unfortunately, recorded in 'grounds'. These include all samples that appeared to form a coherent group as determined by species composition, substrate, and geographic position. Each 'ground' is published as one sample with species listed in a semi-quantitative fashion. The original data have since been lost (Holme, pers. comm. 1982). Ford (1923) published details of 64 samples but 70 other samples from the same areas were not published as they were not comparable for sampling reasons (*in litt.* Ford 1953). These 70 extra samples can, however, be compared on a semi-quantitative or presence/absence level (Table 2).

Identification

Almost all taxa have been identified to species level. An exception to this is *Nucula*, for which all authors have only recorded one species, but each of the pre-1953 identifications is of different species. It is most unlikely that species occurrence would go by survey and therefore all have been grouped as *Nucula* sp. Similarly, all species of *Anomia* have been grouped because of the difficulty of identifying dead separated valves. *Trivia* is now considered as two species, where formerly it was one, and the prior case is adhered to. The two genera of synaptids (Holothuria) are treated as one taxon. When dealing with the earlier faunal records many of the taxa have undergone revision and in all cases we follow the Plymouth Marine Fauna (Marine Biological Association 1957). For this

TABLE 1. Details of the surveys of marine benthos off Plymouth, which provided the data for this study.

	Allen 1889	Crawshay 1912	Ford 1923	Smith 1932	Holme 1953	Holme 1961–1966	Probert 1973	This paper
Author Publication	Allen 1889	Crawshay 1912	Ford 1923	Smith 1932	Holme 1953	Holme 1961–1966	Probert 1973	This paper
Sampling period	Summers 1895–1898	1906	May 1922–June 1923	1931	Summer 1950	July–Dec. 1959, Jan. 1962	April 1972	Sept. 1980–May 1981
Area sampled	Eddystone –start Pt.	SW. Eddystone	Plymouth–Eddystone–Bigbury Bay	Eddystone	Plymouth–Eddystone	Looe–Start Pt., S. Eddystone	Bibury Bay	Plymouth Stoke Pt., Eddystone
Number of samples	18 grounds 95 stations	63	134 (64 published)	24	20	31 (1961–25) (1966–6)	7	57
Sampling technique	Naturalist's dredge, Otter and Beam trawls	44 cm, 92 cm, 107 cm triangular dredges, Otter trawl	$0.1\ m^2$ grab, · ×10 for one sample	0.1^2 grab, Naturalist's and Conical dredges	0.1^2 double scoop grab, ×5 for one sample	$\leqslant 21$ Anchor dredge	Smith and McIntyre grab	10L Modified Naturalist's dredge
mech size	—	—	1·2 mm	1·5 mm	2·2 mm	2·2 mm	—	2 mm
Substrates	Sands and gravels	Very few records, sands and gravels	Muds, sands, and shell-gravels	Rock, shell-gravel	Muddy sands, sands gravels	Muddy sands, sands, shell-gravels	Muddy and clean sands	Shell-gravels
Faunal record	Semi-quantitative, quantitative	Semi-quantitative, quantitative	Quantitative	Quantitative	Quantitative	Quantitative semi-quantitative	Quantitative	Quantitative

TABLE 2. Table indicating the different methods of recording faunal occurrences used by different authors in their published data. Thus Ford (1923), Smith (1932) . . . etc. in column 1 published quantitative data. Allen (1899) and Holme (1966) recorded their data as listed in columns 2 and 3. To compare results from the surveys in columns 1–3 the data were transformed to quantitative (column 4), semi-quantitative (5), or qualitative (6) states.

Published (original) date			Transformed data		
1 Quantitative Abundance is published by the underlisted authors	2 Allen (1899), some of Crawshay's (1912)	3 Holme II (1966)	4 Quantitative	5 Semi-quantitative	6 Qualitative
Ford (1923)	0	0	0	0	0
Smith (1932)	1	1–2	1	1 ⎫	
Holme I (1953)	few	3–9	5	2 ⎪	
Holme II (1961)	numerous	10–99	55	3 ⎬	1
Probert (1973)	abundant	100	550	4 ⎪	
This survey	—	—	5500	5 ⎭	

study each species has been assigned a number which is in the order that species appear in the Plymouth Marine Fauna (see Appendix 1).

Statistical analysis

Because of the size of the data (185 taxa and 379 samples) and the many different ways in which comparisons are to be made, multivariate statistical analysis was considered essential. Several multivariate methods are now in common usage in the analysis of species/samples matrices including Principal Components Analysis, Polar Coordination, Correspondence Analysis, and Detrended Correspondence Analysis. All of these methods display results as eigenvalue plots whereby species with the most similar occurrences or samples with the most similar species plot close together. The most dissimilar species and samples, in contrast, plot far apart. The relative merits of these methods have been discussed by Gauch et al. (1977), Gauch (1982), Hill (1973, 1974), Hill and Gauch (1980), and Orloci (1978). They are also compared with examples by Spicer and Hill (1979) and Spicer (1981). The latter authors consider Correspondence Analysis (Hill 1973) to be most suitable for species/sample data as plots of these are complementary. A brief non-mathematical explanation of the technique is given in Hill (1973) and Spicer and Hill (1979). Detrended Correspondence Analysis (DECORANA: Hill 1979) is an improved version of Correspondence Analysis.

The program gives eigenvalues for the first four axes and the number of iterations required to reach stability. The eigenvalue gives the amount of variance on each axis up to a maximum of 1·00 on each axis. In practice it was found that most of the variance was accounted for on the first two axes and little further information could be observed from plotting the third or fourth. In Probert's (1973) data, all the variance was confined to the first two axes. Sample scores have been zeroed. Because the sample scores are the mean scores of the species that occur in them, the species scores will have a broader range and there will always be scores below zero for species (Hill 1979). All default options in the program were used except when sample data were transformed.

This technique proved robust and the program simple to run. Some samples had to be removed because they showed so much variation that all other samples clustered together. For example, sample 339 contained just five Ensis siliqua, a species found only at four out of the remaining 378 stations. The program allows entry of quantitative data, which, once entered, can be transformed to semi-quantitative or presence/absence form (Table 2) prior to analysis. The quantitative state was only used in an analysis of our data and those of Ford (1923). A semi-quantitative transformation (Table 2) was used for the majority of analyses. The intermediate abundances were

calculated linearly between the desired semi-quantitative scores (e.g. 10–2·1). Abundances greater than 5500 (only found in the 'dead' data) were all transformed to 5. The DECORANA program was entered and run on the CDC computer at Imperial College, London.

COMMUNITY COMPOSITION AND DISTRIBUTION

Our data have been analysed in a number of ways to study the relationships between the live and dead faunas of the shell-gravels. First, the entire past and Recent live and dead species occurrences have been compared semi-quantitatively (text-figs. 3 and 4A). Information from this analysis compared the shell-gravel community with those from the surrounding sea-floor and the dead fauna from the shell-gravels. Secondly, the occurrences of bivalves have been analysed as they represent the dominant components of both the live and dead faunas (text-figs. 4B, C, 5, 6). Thirdly, our live and dead faunas from the shell-gravels were analysed quantitatively to study in detail the live fauna and its relation to today's dead fauna (text-fig. 7).
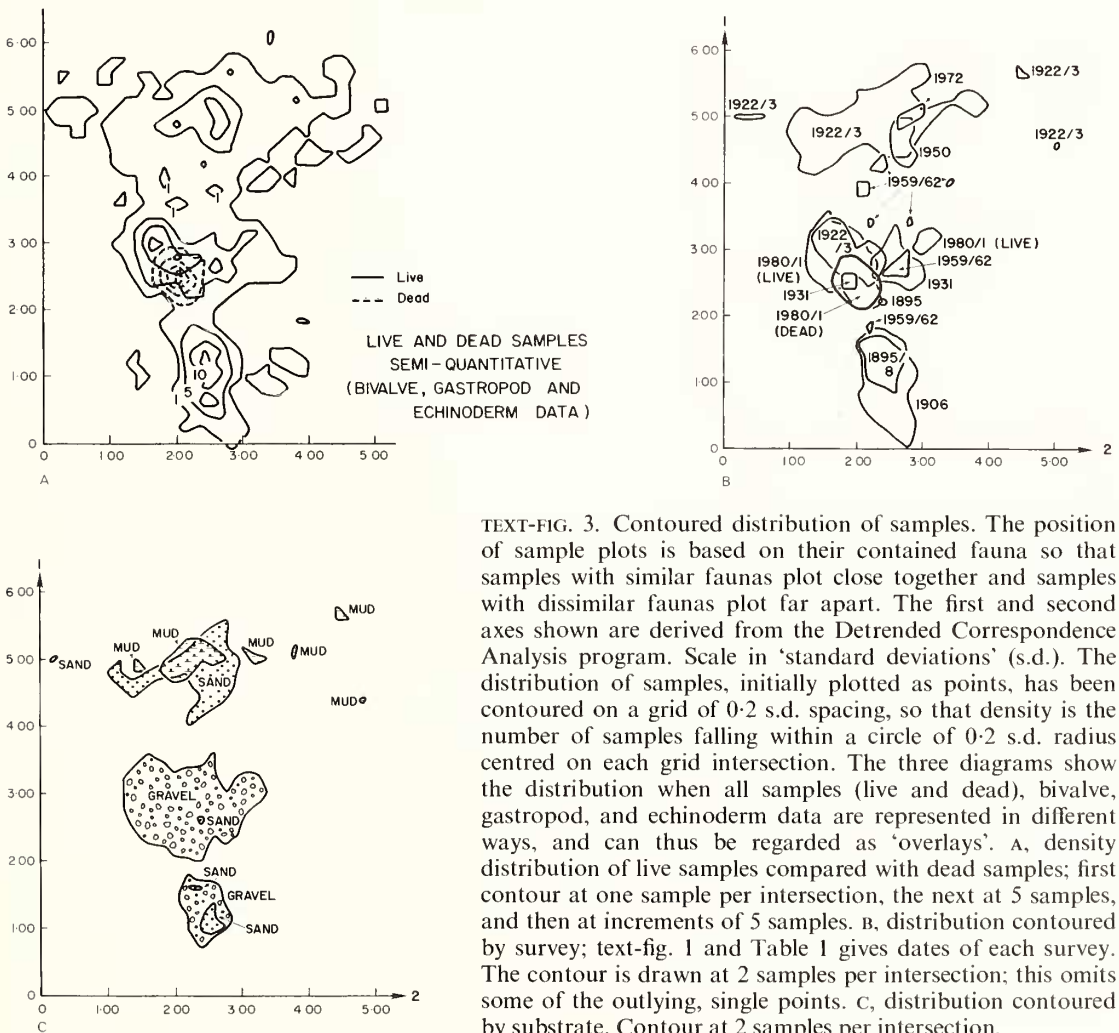
TEXT-FIG. 3. Contoured distribution of samples. The position of sample plots is based on their contained fauna so that samples with similar faunas plot close together and samples with dissimilar faunas plot far apart. The first and second axes shown are derived from the Detrended Correspondence Analysis program. Scale in 'standard deviations' (s.d.). The distribution of samples, initially plotted as points, has been contoured on a grid of 0·2 s.d. spacing, so that density is the number of samples falling within a circle of 0·2 s.d. radius centred on each grid intersection. The three diagrams show the distribution when all samples (live and dead), bivalve, gastropod, and echinoderm data are represented in different ways, and can thus be regarded as 'overlays'. A, density distribution of live samples compared with dead samples; first contour at one sample per intersection, the next at 5 samples, and then at increments of 5 samples. B, distribution contoured by survey; text-fig. 1 and Table 1 gives dates of each survey. The contour is drawn at 2 samples per intersection; this omits some of the outlying, single points. C, distribution contoured by substrate. Contour at 2 samples per intersection.

Live and dead faunas from shell-gravels and surrounding areas

A semi-quantitative analysis (Table 2) of the fauna from all the surveys together with our dead material is illustrated in text-figure 3. Three main clusters are visible separating out on the first axis. The central cluster, containing samples with intermediate ordinations, is the densest, whilst samples with higher ordinations on axis 1 cluster with considerable variation along the second axis. Because the position of each sample plot is based on the species it contains, neighbouring plots of samples and clusters of samples have similar faunas. Therefore, separate clusters indicate groups of stations with similar faunal associations. The location of samples and the occurrence of clusters can be discussed with respect to the possible causes of clustering such as a faunal change through time, substrate differences, water depth, etc. A simple, graphical way of comparing the importance of these various controls is by constructing overlays which contour author's samples (text-fig. 3B), substrate types or depths (text-fig. 3C).The contouring of samples by author/time (text-fig. 3B) indicates that no single sampling programme coincides with one cluster. The uppermost cluster comprises samples from Ford (1923), Holme (1961, 1966), and Probert (1973). The lowest cluster contains stations of Allen (1899), Crawshay (1912), and Holme (1961, 1966). The central cluster contains samples collected by Allen (1899), Ford (1923), Smith (1932), Holme (1961, 1966), and our live faunas from the shell-gravels. In addition, this central cluster contains our samples based on dead shell-gravel faunas which plot in a restricted area within this cluster. This indicates that similar faunas have been retrieved by different authors, sampling at different periods of time. Also, it indicates that our dead fauna is similar to live faunas sampled over the last ninety years. This contouring also allows us to see that the different sampling techniques and recording, together with our transformation of these data, are not responsible for the clustering of stations (but see Allen (1899) and Crawshay (1912) below). The central cluster, for example, contains samples from a range of dredges, grabs, semi-quantitative, and quantitative recording of data (Table 1).

The important effect of substrates on faunal occurrences has been studied by indicating the sediments recorded at each station (text-fig. 3C). As various authors have used different quantitative or descriptive terms for describing substrates and these have had to be compared, only the following substrate categories were used: muds ('mud', 'sandy mud', 'muddy sand'), sands ('silty sand', 'sand'), and gravels ('shelly-gravel', 'coarse shelly-gravel'). Other ambiguous terms (e.g. 'sand and shell' or 'mud, sand, gravel, and shell') have not been used. Unfortunately, Crawshay (1912) made few records of substrate types.

When sample and substrate clusters are compared (text-fig. 3A, C) there is a very close correlation. The dense central cluster is almost entirely made up of faunas from the inshore and Eddystone shell-gravels. Similarly, the lower cluster is mostly offshore shell-gravels and sands. The upper cluster consists of muddy stations (with high ordinations on axis 2) and sandy stations (with low ordinations on axis 2) with an overlap in the centre.

Water depth has a similar pattern to substrate as there is a direct, but imprecise, relation between the two in this area of the Channel. Grain size generally decreases inshore. Finer particles are apparently winnowed in the offshore and deposited in sheltered nearshore sites. However, inshore there are also sand and gravel areas. The difference between the samples from the central and bottom clusters is in water depth and distance from shore. The lower clustered sands and gravels samples by Allen (1899) and Crawshay (1912) are from more offshore sites (text-fig. 1B) then the Eddystone and inshore (Plymouth Sound and Stoke Point) shell-gravels of the central cluster. Apart from this separation there is no other pattern which may be explained by the spatial siting of samples. Therefore, the main control on clustering of stations appears to be substrate type as has been commented on by previous authors (Ford 1923; Jones 1950; Holme 1966).

The other principle way of analysing these data is to study species occurrences (see Methods). For this analysis, rare species (occurring in less than five of the 354 live samples) are omitted as are those species which do not show a substrate preference. Substrate preference was defined here as those species which occur more than 50% of the time in any one substrate.

When occurrences of species are analysed (text-fig. 4A), a pattern similar to that displayed with substrate appears. Both the living species on sand and, to a lesser extent, the living species on
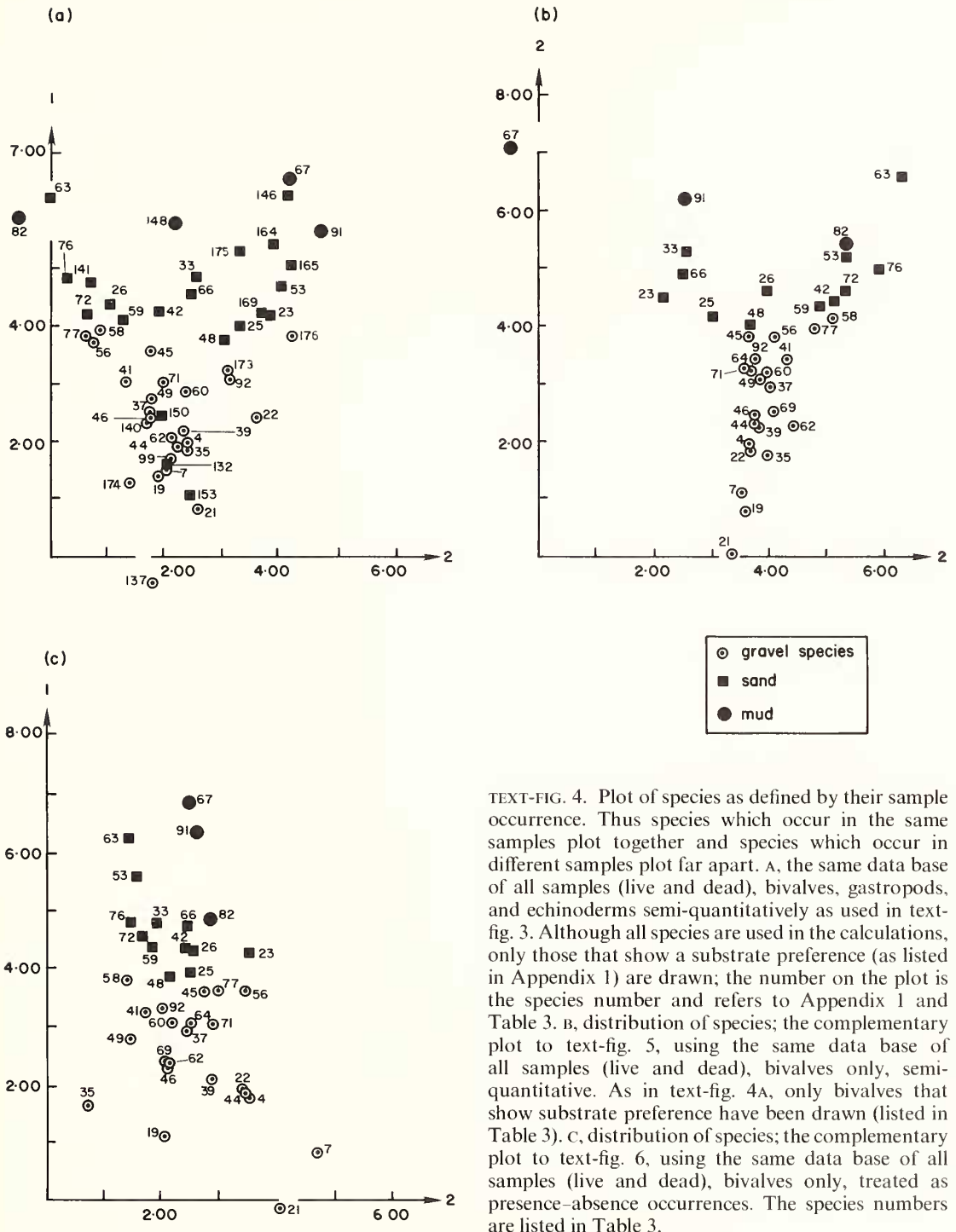
TEXT-FIG. 4. Plot of species as defined by their sample occurrence. Thus species which occur in the same samples plot together and species which occur in different samples plot far apart. A, the same data base of all samples (live and dead), bivalves, gastropods, and echinoderms semi-quantitatively as used in text-fig. 3. Although all species are used in the calculations, only those that show a substrate preference (as listed in Appendix 1) are drawn; the number on the plot is the species number and refers to Appendix 1 and Table 3. B, distribution of species; the complementary plot to text-fig. 5, using the same data base of all samples (live and dead), bivalves only, semi-quantitative. As in text-fig. 4A, only bivalves that show substrate preference have been drawn (listed in Table 3). C, distribution of species; the complementary plot to text-fig. 6, using the same data base of all samples (live and dead), bivalves only, treated as presence–absence occurrences. The species numbers are listed in Table 3.

gravel plot in distinct fields. The gravel, sand, and mud species as defined by this analysis are similar to substrate/species lists of Ford (1923) and Holme (1966) and are presented in Table 3.

The majority (29 out of 50) of the taxa which are not substrate specific by our definition (above) are taxa which appear to avoid gravel (i.e. occur in sands and muds, e.g. *Thyasira flexuosa*) or appear to avoid muds (i.e. occur in sands and gravels, e.g. *Aequipecten opercularis* and *Ophiothrix fragilis*). The remaining taxa have too few occurrences (5–9) or too little substrate data for any meaningful pattern to emerge.

When viewing both the sample (text-fig. 3) and species (text-fig. 4) plots the shell-gravels and their faunas plot as distinct fields. The substrate plot (text-fig. 3c) contains both the inshore areas of Plymouth Sound, Stoke Point, and Bigbury Bay together with those from Eddystone. This confirms the distinctness of this fauna through time and the commonest members of this community are listed in Table 3.

The observation of major palaeoecological importance, however, is that the dead fauna plots centrally within this cluster and therefore gives a good representation of the community over at least the last ninety years. These samples are not only similar to one another but their ordination indicates an averaging of the fauna over the last ninety years. The dead fauna can therefore be described as 'time-averaged' in the sense of Walker and Bambach (1971) or Warme *et al.* (1976). The author (or time) contouring of the shell-gravel samples (text-fig. 3b) illustrates shifts in faunal dominance over the last ninety years.

The earliest surveys (Allen 1899; Crawshay 1912) have low ordinations on axis 1 and these samples have relatively few infaunal molluscs but are dominated by epifaunal *Anomia* spp. (species number 11), *Solaster papposus* (155), *Marthasterias glacialis* (158), *Ophiactis balli* (161), and *Echinus*

TABLE 3. Substrate preferences of fauna (species occurring at five or more samples, 50% or more of which are in any one substrate). Numbers refer to species list (Appendix 1) and text-fig. 4.

Gravel species	Species No.	Sand species	Species No.	Mud species	Species. No.
Glycymeris glycymeris	4	*Modiolus barbatus*	6	*Abra nitida*	67
Modiolus phaseolinus	7	*Arctica islandica*	23	*Mya truncata*	82
Lima loscombi	19	*Diplodonta rotundata*	25	*Thracia convexa*	91
Astarte sulcata	21	*Lucinoma borealis*	26	*Philine* sp.	148
A. triangularis	22	*Acanthocardia echinata*	33		
Laevicardium crassum	35	*Dosinia lupinus*	42		
Cardium scabrum	37	*Venerupis aurea*	48		
Gouldia minima	39	*Mysia undata*	53		
Dosinia exoleta	41	*Gari fervensis*	59		
Venus casina	44	*Mactra stultorum*	63		
V. ovata	45	*Abra prismatica*	66		
V. fasciata	46	*Hinia reticulatus*	141		
Venerupis rhomboides	49	*Cylichna cylindracea*	146		
Lutraria augustior	56	*Astropecten irregularis*	150		
Gari costulata	58	*Anseropoda placenta*	153		
G. tellinella	60	*Amphiura filiformis*	164		
Solecurtus scopula	62	*Acrocnida brachiata*	165		
Spisula solida	64	*Echinocardium cordatum*	176		
Arcopagia crassa	69				
Tellina pygmaea	71				
Ensis arcuatus	77				
Thracia villosiuscula	92				
Calliostoma zizyphinum	99				
Hinria incrassata	140				
Echinocyamus pusillus	174				

esculentus (171). This is clearly different from all later surveys which show a predominance of infaunal bivalves (Table 3). It is possible here that the infauna was not well sampled because of the use of an unmodified Naturalist's dredge. This is the only indication we have of sampling procedure affecting our results. The later survey of Ford (1923) sampled gravels with a similar fauna to that found today dominated by: *Musculus marmuratus, Parvicardium ovale, Callista chione, Venus ovata, V. fasciata, Venerupis rhomboides, Lutraria angustior* (*L. magna* of Ford), *Gari costulata, G. tellinella, Spisula elliptica, Tellina pygmaea, Ensis arcuatus,* and *Lunatia alderi.*

Workers in the intervening periods (Smith 1932; Holme 1966) sampled a community resulting in higher ordinations on the second axis. Smith's (1932) centrally plotting samples are dominated by *Lima subauriculata, Astarte triangularis, Gouldia minima, Venus fasciata, Ophiura texturata,* and *Echinocyamus pusillus.* Similarly Holme's (1966) samples are characterized by *Aequipecten opercularis, Thracia villosiuscula, Calliostoma papillosum, Asterias rubens, Ophiocomina nigra, Amphiura chiajei, Ophiura albida,* and *Pseudocucumis mixta.*

The samples of dead material from the three shell-gravel sites overlap almost completely with the samples of the live faunas from these areas. The common live and dead taxa from these centrally clustering samples include: *Glycymeris glycymeris, Aequipecten opercularis, Cardium scabrum, V. ovata, Venerupis rhomboides, Gari tellinella, Gouldia minima, Tellina donacina, T. pygmaea, Arcopagia crassa, Venus casina, Laevicardium crassum, Cytharella linearis,* and *Nucella lapillus,* all of which are regarded as typical of the Boreal offshore gravel community of Jones (1950).

The tight grouping of the dead samples appears to result also from a gastropod dominated dead fauna which are not recorded live: *Diadora* sp., *Acmaea virginea, Tricolia pullus, Alvania punctura, Rissoa inconspicua. R. parva, R. membranacea, Bittium reticulatum, C. coarctacta,* and *Gibbula cineraria;* and bivalves *Notirus irus* and *Sphenia binghami.* This fauna dominated by dead gastropods has also been recorded in previous studies of this nature (Cadée 1968; Bosence 1976). The evidence suggests that the gastropods arrive on storm-derived weed from nearby rocky areas. Many of the shells are small and robust and probably last a long time in the shell-gravels. In addition to the above exotic taxa there are some molluscs in the dead fauna which are normally found in muddy or sandy substrates: *Thyasira flexuosa, Abra prismatica, Spisula subtruncata, Venurupis aurea, Nucula* sp., *Corbula gibba, Turritella communis,* and *Lunatia alderi.* These exotic taxa may represent transported shells or short-term fluctuations in the live community not recorded in the faunal surveys of muddy or sandy patches within the shell gravels. The latter explanation is considered more likely as these patches are seen in bottom photographs, some of these shells are thin and fragile and unlikely to survive much transport and there is a good historic record of the fauna from this area.

The shell-gravel community and death assemblage can, therefore, be seen to be distinct from the communities of the surrounding sea-floor areas. The Boreal offshore sand association (Jones 1950; Holme 1966) accounts for many of the station plots with high axis 1 ordinations and low axis 2 ordinations. Similarly, the Boreal offshore muddy sand association is present in stations with high ordinations on axes 1 and 2.

Although the shell-gravel community has fluctuated in faunal dominance over the last ninety years, the accumulating dead shelly fauna provides an accurate record of the time averaging of the live fauna.

Live and dead bivalve faunas; semi-quantitative data

Because of the poor preservation potential of the echinoderms as macrofauna and the over-representation of gastropods in the dead fauna, it was considered useful to carry out comparisons of all stations using only the bivalve fauna. A semi-quantitative analysis of these data (text-figs. 4B, 5) indicates that the bivalves on their own can be used in the differentiation of present-day substrate-defined communities and that the shell-gravel community is well represented in the dead material. The clustering along the first axis (text-fig. 5A, B, C) is very similar to that of the combined mollusc and echinoderm fauna and both eigenvalues have almost the same variance as before indicating little loss of information. The position and nature of clusters is similar to those from the
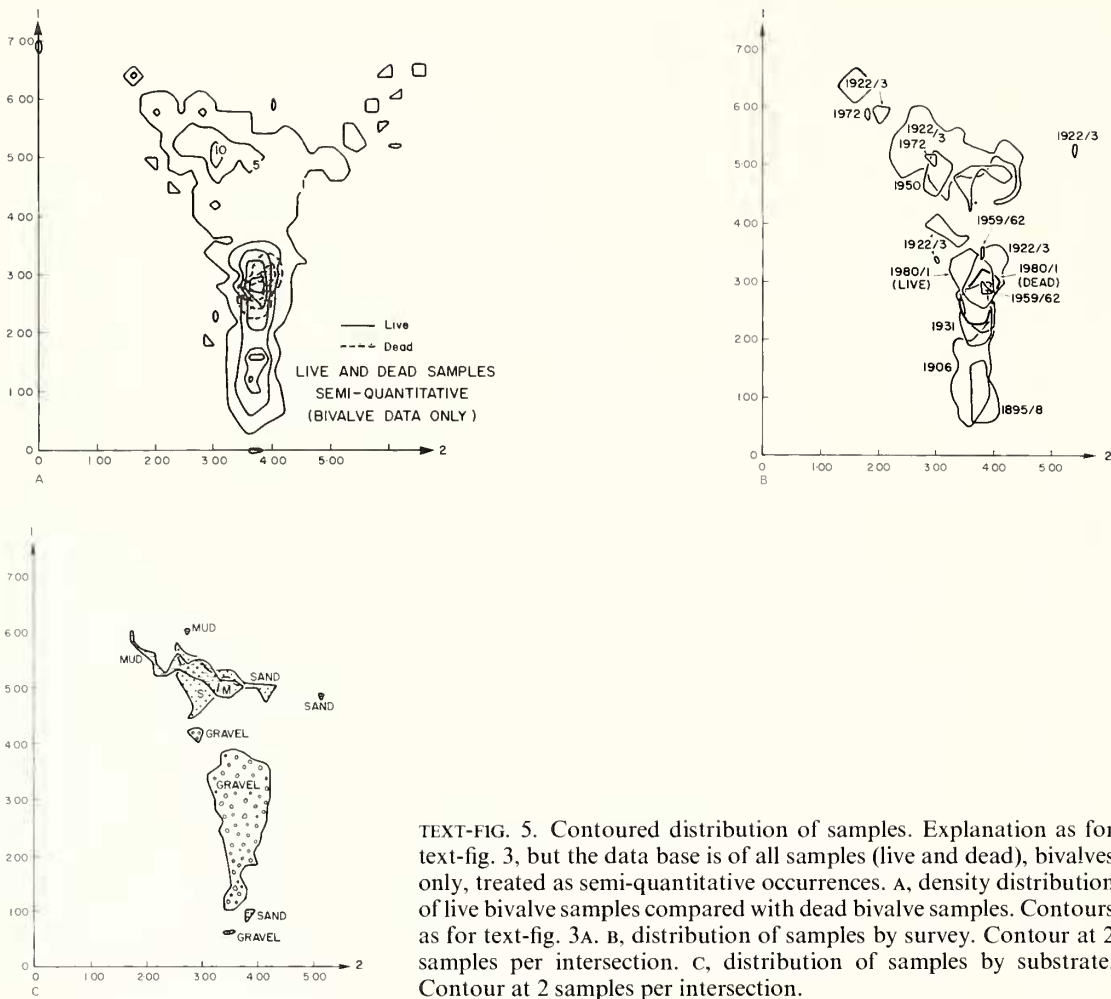
TEXT-FIG. 5. Contoured distribution of samples. Explanation as for text-fig. 3, but the data base is of all samples (live and dead), bivalves only, treated as semi-quantitative occurrences. A, density distribution of live bivalve samples compared with dead bivalve samples. Contours as for text-fig. 3A. B, distribution of samples by survey. Contour at 2 samples per intersection. C, distribution of samples by substrate. Contour at 2 samples per intersection.

previous analysis with highest ordinating stations on axis 1 being the sand and mud substrate stations of Ford (1923), Holme (1961, 1966), and Probert (1973). Axis 2 again separates out mud (with low ordinations) and sand (with high ordinations) stations with considerable intermediate overlap. The inversion of the ordinations compared with previous analyses (text-figs. 3, 4B) is not significant as it is only the relative distance apart of the stations which indicate similarities and differences.

The shell-gravel stations remain as separate clusters (text-fig. 5B, C) with the more offshore sands and gravels of Allen (1899) and Crawshay (1912) plotting the low ordinations on axis 1.

The dead bivalve samples (text-fig. 5A) completely overlap the spread of live faunal samples from the shell-gravels. The common fauna of the central samples of the live and dead bivalves is: *Venus ovata*, *Tellina pygmaea*, *Gari tellinella*, *Venerupis rhomboides*, *Arcopagia crassa*, *Venus fasciata*, *Glycymeris glycymeris*, and *T. donacina*. The spread of our live faunal samples from the central cluster is by samples with abundant *S. elliptica*, and, to a lesser extent, *Laevicardium crassum* and *Lutraria angustior*. Smith's (1932) samples have lower axis 1 ordinations caused by the occurrence of *Astarte triangularis* together with *Modiolus barbatus*, *M. phaseolinus*, *Aequipecten opercularis*,

Lima subauriculata, and *Astarte sulcata*. Ford's (1923) stations ordinate high on both axes away from the central cluster by the occurrence of the following, often sand-living, taxa: *Dosinia lupinus*, *S. subtruncata*, *C. gibba*, *Callista chione*, and *Parvicardium ovale*. In palaeoecological studies, it is usually assumed that the total fauna should be assessed to differentiate benthic communities. Here, the evidence suggests that, in the absence of data on other groups, the benthic communities can be differentiated using only the bivalves.

Presence–absence data

The data on bivalve occurrences have been transformed to a qualitative state (Table 2) to evaluate the effect that this loss of information may have on community recognition. The analysis is presented in text-figures 4c and 6. Again, the samples can be seen to occur in three clusters separating out along the first axis. However, in this case the sand and mud samples are no longer differentiated on the basis of their faunas and therefore the boreal offshore sand and muddy sand associations can no longer be recognized.

The shell-gravel faunas, however, still plot as a separate cluster with Smith's (1932) samples
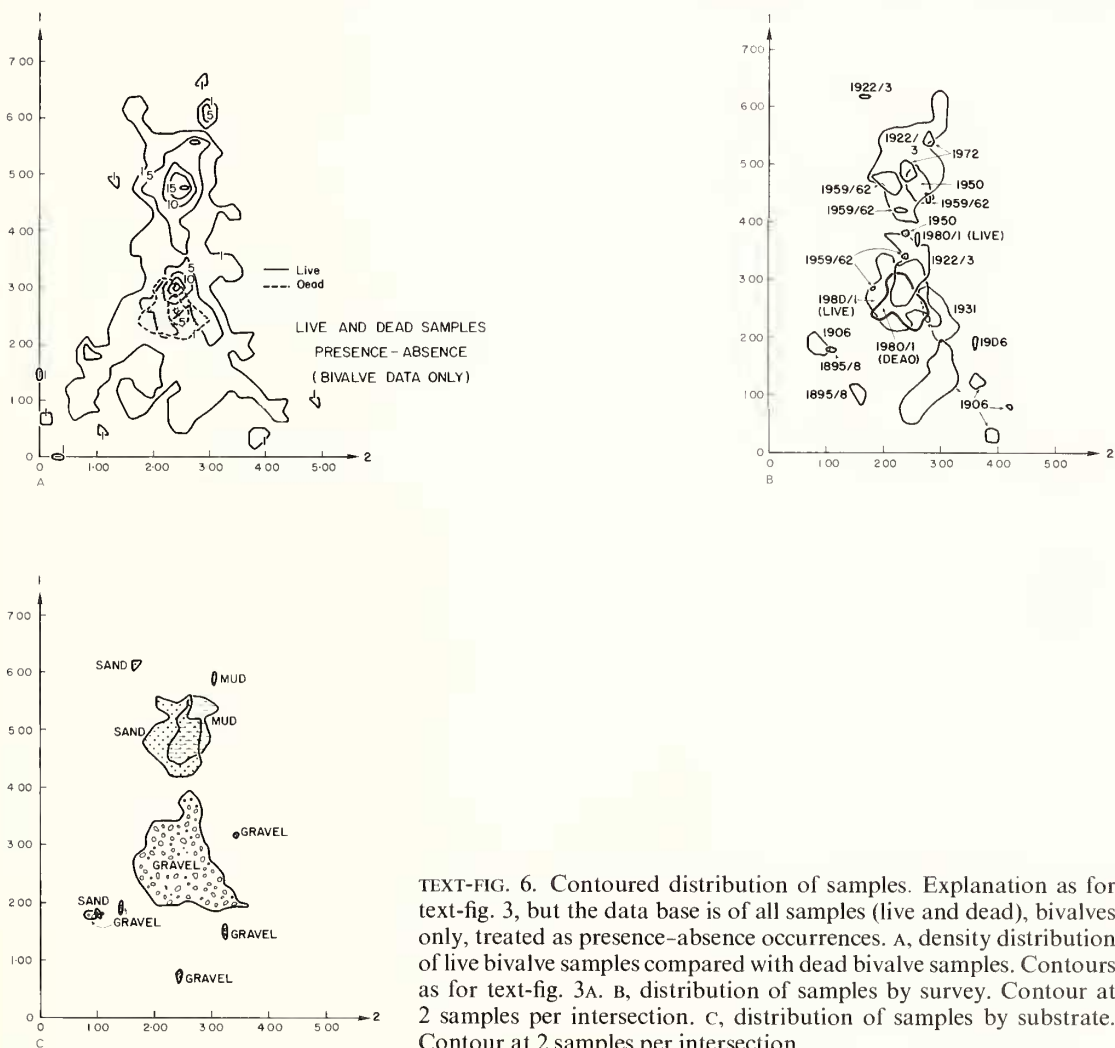
TEXT-FIG. 6. Contoured distribution of samples. Explanation as for text-fig. 3, but the data base is of all samples (live and dead), bivalves only, treated as presence–absence occurrences. A, density distribution of live bivalve samples compared with dead bivalve samples. Contours as for text-fig. 3A. B, distribution of samples by survey. Contour at 2 samples per intersection. C, distribution of samples by substrate. Contour at 2 samples per intersection.

plotting slightly off-centre (through the presence of *A. triangularis* and *Gouldia minima*). Allen's (1899) and Crawshay's (1912) offshore dredge samples remain distinct.

The results presented here indicate that there is considerable information in the qualitative data in that some of the live communities are differentiated and the live and dead bivalve faunas are very similar. The evidence therefore suggests that in the absence of quantitative data considerable information can still be obtained from qualitative data and its use should not be discounted. Buzas (1972) came to similar conclusions when comparing quantitative and qualitative data on foraminiferal distributions. The relative merits of these methods of analysis is discussed further in Spicer (1981).

Present-day live and dead shell-gravel faunas

The analysis compares the present-day shell-gravel faunas sampled quantitatively by us in 1980–1981. The raw data indicate that whilst the bivalves are well represented in both the live and dead faunas there are few live gastropods (*Gibbula umbilicus*, *Lacuna pallidula*, and *Lunatia alderi*) or echinoderms (*Astropecten placenta*, *Asterias rubens*, *Echinocyamus pusillus*, and *Spatangus purpureus*). However, dead gastropods are abundant and at Eddystone, twenty-two species are found dead but none alive. The dead echinoderm fauna is always dominated by *E. pusillus*.

The diversity (species numbers) of the bivalves can be compared from the three shell-gravel sites (Plymouth Sound, Stoke Point, and Eddystone) as sample sizes are constant. The fewest samples were taken at Stoke Point (12 live and 7 dead) and therefore these can be compared with faunas from the same numbers of samples from other areas (Table 4).

These figures confirm, along with other studies, that the diversity of the dead fauna is higher than that of the live. It can also be seen that the Eddystone faunas today are considerably less diverse than the Plymouth Sound and Stoke Point faunas.

At any one site only a few species are living abundantly. *Glycymeris glycymeris* (max. 46 individuals) is abundant at Stoke Point whilst *Spisula solida* is abundant in all samples from Plymouth Sound (max. 2430). This was also found to be the case in 1923 when Ford sampled here. At Eddystone *V. fasciata* (max. 10) and *G. glycymeris* (max. 7) are the most abundant. These bivalves were also abundant in Ford's (1923) survey but were only occasionally found by Allen (1899).

TABLE 4. Average occurrence of the live bivalve fauna in shell-gravels from the survey of 1980–1981. Data have been combined and averaged for samples taken in November 1980, January, March, May 1981. The average occurrence of each live species, and the standard deviation thereof, is compared between the three areas sampled. Specimens marked * are unique to the area concerned.

Plymouth Sound (15 samples)	Av./10 l	s.d	Stoke (12 samples)	Av./10 l	s.d.	Eddystone (13 samples)	Av./10 l	s.d.
Spisula elliptica	309	(650)	Glycymeris glycymeris	6	(13)	Venus fasciata	2·3	(3·1)
Venus fasciata	14	(11)	Venus fasciata	3·6	(3·4)	Nucula hanleyi	1·6	(1·6)
Venerupis rhomboides	4	(5)	V. ovata	3·5	(3·1)	Gouldia minima	1·2	(1·2)
Nucula hanleyi	3	(5)	Nucula hanleyi	1·1	(1·9)	Glycymeris glycymeris	0·92	(1·5)
Venus ovata	1·5	(1·7)	Tellina crassa	1·1	(2)	Venerupis rhomboides	0·58	(1·5)
Tellina pygmaea	1	(2)	Gari tellinella	0·91	(1·5)	Venus casina	0·58	(1·5)
Gari tellinella	1	(2·3)	Gardium scabrum	0·5	(1)	V. ovata	0·5	(1·17)
Laevicardium crassum	0·62	(2·5)	Laevicardium crassum	0·41	(0·9)	Thracia villosiuscula	0·42	(1·4)
*Cardium exiguum	0·62	(2·5)	Venerupis rhomboides	0·38	(1·1)	Arcopagia crassa	0·25	(0·62)
Arcopagia crassa	0·56	(1·4)	Tellina pygmaea	0·25	(0·86)	Spisula solida	0·16	(0·57)
Gouldia minima	0·18	(0·75)	Gouldia minima	0·25	(0·86)	Tellina donacina	0·16	(0·57)
*Ensis sp. (juv.)	0·18	(0·54)	Venus casina	0·08	(0·28)	Laevicardium crassum	0·08	(0·28)
Cardium scabrum	0·12	(0·3)				*Pecten maximus	0·08	(0·28)
Glycymeris glycymeris	0·12	(0·5)						
*Lutraria angustior	0·06	(0·25)						

The dead assemblage is both more diverse and more abundant and many species occur in hundreds and some in thousands within each 10 l sample. *S. solida* dominates the Plymouth Sound death assemblage (average 3011 individuals per sample) but is less common elsewhere (28/sample at Eddystone and Stoke Point). Conversely the following are very abundant (over 500/sample) at Eddystone: *Anomia* sp., *Pallolium tigerinum*, *P. simile*, *Cardium exiguum*, *Gouldia minima*, *V. ovata*, and *V. fasciata* but only occur in tens from the other two areas.
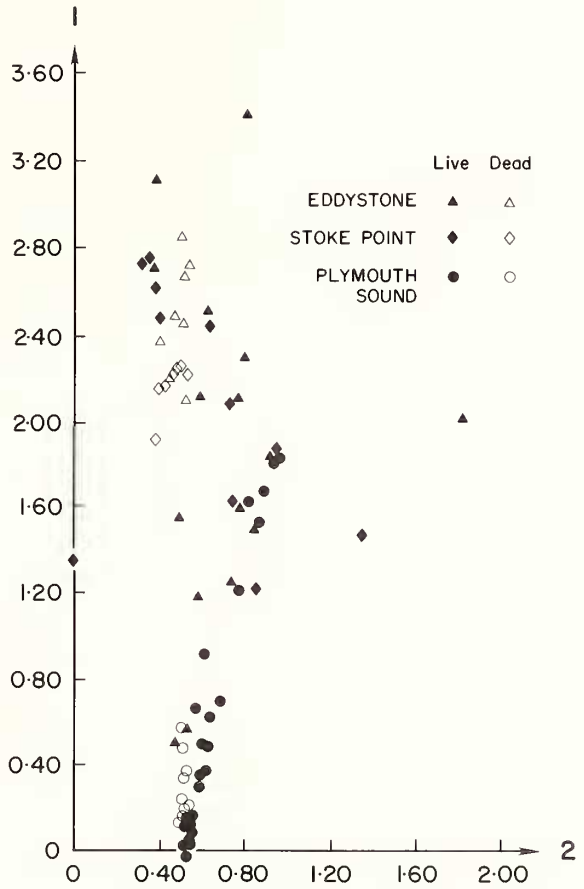
TEXT-FIG. 7. Distribution of samples in shell-gravels based on contained species. The first and second axes are derived from the Detrended Correspondence Analysis program, and the scale is in standard deviations. The data base is made up of samples from the last survey, of 1980–1981, of live and dead samples of bivalves, treated fully quantitatively. The plot shows the relation between provenance of the samples, and live and dead bivalve numbers.

Although visual assessment of the raw data picks out some of the differences between the bivalve faunas from these three shell-gravel sites when the total faunal occurrences are compared by correspondence analysis, they are found to have a considerable amount of similarity. The fully quantitative comparison of live and dead faunas from these three areas is illustrated in text-figure 7. The three areas plot in overlapping fields spread by variation along axis 1. This coincides with shallow-to-deep water and inshore to offshore variation from Plymouth Sound (low ordinations) to Eddystone (high ordinations).

When the shell-gravel fauna is viewed on its own and not in relation to faunas from the surrounding substrates, it is seen that the dead fauna does not plot as a single central grouping but plots with the live fauna from that area. Therefore, when considered in relation to the surrounding faunas the live and dead shell-gravel community is a distinct grouping: when considered in isolation each area has its own live faunal variation which is reflected in the accumulating shelly material.

Qualitative and semi-quantitative comparisons of the faunas from these three areas were also undertaken. These analyses show a similar separation of the live faunas but the dead faunal separation is lost and all dead faunal samples plot in a separate field with little variation. These analyses stress the importance of quantitative palaeoecological data to obtain the maximum information concerning the live fauna.

DISCUSSION

This analysis demonstrates a considerable degree of confidence in community reconstruction from dead material because the relative abundances of the time-averaged living species are preserved in the dead assemblages. This result differs from our previous work (e.g. Bosence 1979a, b) because of scale. When communities are sampled in detail on a scale of tens of hundreds of metres, with sampling over a short period (less than a year), then major differences between live fauna and dead material are found. There appears to be considerable post-mortal mixing from adjacent areas and from different live faunas. If, however, the sampling is on a larger scale, of kilometres or tens of kilometres and over a long period of time, then the correspondence between live and dead faunas becomes more precise; the fluctuation and vagaries of live populations have been ironed-out. The dead fauna may bear no relation to any community at any one instant, but to the community's median position over a period of time; or, 'time-averaged' in the sense of Walker and Bambach (1971).

The presentation of these fluctuations in community composition will depend on sedimentation rates. Although sedimentation rates from the English Channel shell-gravels have not been studied, data from algal gravels from the west or Eire, which have many taxa in common (Bosence 1976, 1980) have molluscan production rates of 15 g/CaCO$_3$/m²/yr. Assuming density of material of 2·5 g/cm³ and 60% porosity, this would give rise to an accumulation rate equivalent to 6 mm every 100 years. Therefore one shell thickness may have been deposited during the eighty-year period of sampling in these shell-gravels. Farrow et al. (1984) give similar rates for shell-gravels from the Scottish shelf averaging 3–31 mm/100 yrs. Very slow sedimentation rates are also suggested from the radiocarbon dating of shells from the British shelf carried out by Wilson (1982) and Sturrock (1982) who have dates ranging from 10 920 ± 150 to 960 ± 50 years B.P.

This information on sedimentation rates illustrates the impossibility of preserving information on population fluctuations or on any biotic interactions (cf. McCall and Tevesz 1983). A caveat must arise here as to the limits of the usefulness of time-averaged data; whilst soft substrate 'communities' may be recognized, and possibly their long-term changes recognized, the dynamic nature of communities will be lost.

The fluctuations in the benthic fauna recorded over the last ninety years coincide with fluctuation in the planktonic communities in the Western Channel. Southward (1962, 1980) records a *Sagitta elegans* community in the 1920s which was replaced by *S. setosa* in the 1930s to 1960s. The Celtic Sea *S. elegans* community reappeared in the late 1960s and has continued to today. The changes in planktonic communities have been correlated with changes in water temperature in the Western Channel (Southward 1980) with *S. elegans* inhabiting the warmer Celtic sea waters. Holme (1983) has shown how the arrival of predatory starfish (*Luidia ciliaris* and *L. sarsi*) in the late 1960s possibly from the Celtic Sea is thought to have caused a decline in *Ophiothrix* beds in this area. Our data indicate fluctuations in faunal dominance coincident with these previously recorded changes.

CONCLUSIONS

1. Three major communities can be recognized by multivariate statistical analysis of semi-quantitative faunal records from the area offshore from Plymouth. These are the 'Boreal offshore muddy sand', 'Boreal offshore sand' (Jones 1950), and the shell-gravel communities.

2. The above communities can also be differentiated on the basis of the bivalve fauna only. The

shell-gravel community can be differentiated from the sand and mud communities using just the presence/absence data of the bivalves.

3. The dead shell-gravel faunas are indistinguishable from the live shell-gravel faunas in this analysis and therefore the shell-gravel community is being preserved as a distinct and recognizable assemblage. This agrees with Holme's (1961, p. 443) statement that: 'There is no evidence that dead shells are transported any appreciable distance from the areas in which they originally lived.'

4. Despite the shifts in the composition of the live faunas over the last ninety years the present-day dead fauna show less spread, or greater homogeneity, than the live faunas. The accumulating death assemblage can be said to be 'time-averaging' (Walker and Bambach 1971) the changing live faunas.

5. The historic records of the live shell-gravel faunas over the last eighty years indicates fluctuating populations with similar faunas in 1932 and 1966, and in 1923 and 1980.

6. There are minor qualitative and quantitative differences between the faunas from the shell-gravel sites of Eddystone, Stoke Point, and Plymouth Sound. A quantitative analysis of live and dead faunas from these three locations indicates a different live fauna and death assemblage from each site, the death assemblages being more similar to the live fauna from each site than to live or dead faunas from other sites, i.e. differences in occurrences and abundances between sites are preserved in the dead faunas.

7. In terms of Wilson's (1982) model of shell-gravel formation this correspondence between live and dead faunas suggests that the gravels are in the mature stage of shell-gravel development. The gravels are inhabited by live fauna which can tolerate the coarse substrate, with additional dead shells derived from nearby rocky areas.

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APPENDIX 1

List of species, authors, and numbers used in faunal analysis (text-fig. 4), together with total live and dead occurrences, occurrence by sample for each author and substrate, and substrate occurrences for each live species.

Species	Live occurrences	Dead occurrences	Allen	Crawshay	Ford	Smith	Holme 1959	Holme 1961, 1966	Probert	This paper	Gravel	Sand	Mud	Unassoc'd
BIVALVIA														
1. *Nucula* sp.	126	24	3	1	49	7	10	5	6	21	31	37	18	19
2. *Striarca lactea* (Linnaeus)	2	25	5			1	1				2			
3. *Arca tetragona* (Poli)	5	8	2	3							2			
4. *Glycymeris glycymeris* (L.)	52	24	3	16	11	11		2		9	39	1	4	
5. *Modiolus modiolus* (L.)	9		7	1							4	5		
6. *M. barbatus* (L.)	1			1							1			
7. *M. phaseolinus* (Philippi)	21	9		19			1	1			7	1		1
8. *Musculus marmoratus* (Forbes)	11	25		7	4						3	3	1	2
9. *Mytilus edulis* L.	2		1		1						1	1		
10. *Ostrea edulis* L.	1	1								1	1			
11. *Anomia* sp.	41	22	11	30							10	5		3
12. *Chlamys varia* (L.)	1		1											
13. *C. distorta* (da Costa)	2	12					2				1	1		
14. *Aequipecten opercularis* (L.)	63	22	18	30	6		1	7	1		17	11	3	11
15. *Pallolium tigerinum* (Müller)	15	21	7	8							5	3		2
16. *P. simile* (Laskey)	2	10				2					2			
17. *Pecten maximus* (L.)	29	4	11	16			1		1		9	3		6
18. *Lima hians* (Gmelin)	2	1	2								1			
19. *L. loscombi* Sowerby	11	4	5	4	2						6	1		2
20. *L. subauriculata* (Montagu)	1					1					1			
21. *Astarte sulcata* (da Costa)	23		4	15		4					12			4
22. *A. triangularis* (Montagu)	18	6				18					18			
23. *Arctica islandica* (L.)	9	1		1	5		2	1				5	2	1
24. *Thyasira flexuosa* (Montagu)	53	3			40		7	2	4			20	20	8
25. *Diplodonta rotundata* (Montagu)	12	6			8			4			1	7	2	1
26. *Lucinoma borealis* (L.)	26	3		1	10		8	7				15	4	7
27. *Myrtea spinifera* (Montagu)	12	3			11			1				1	4	6
28. *Kellia suborbicularis* (Montagu)	9	3	5	4							2	2		3
29. *Lepton squamosa* (Montagu)	3	3					2	1						3
30. *Mysella bidentata* (Montagu)	37				30		1	1	5			17	13	3
31. *Tellimya ferruginosa* (Montagu)	9				7			1	1			4	3	1
32. *T. substriata* (Montagu)	4		3	1							2			1
33. *Acanthocardia echinata* (L.)	49	1	2	1	30		6	9	1		1	27	9	6
34. *Parvicardium ovale* (Sowerby)	9	6			6	3					4	2		3
35. *Laevicardium crassum* (Gmelin)	24	12	6	4	2	1		4		7	15	2		4
36. *Cardium exiguum* Gmelin	2	16			1					1	1			1
37. *C. scabrum* Philippi	17	23			10	1	1				12		1	3
38. *C. tuberculatum* Jeffreys	1			1							1			
39. *Gouldia minima* (Montagu)	34	23	1	2	7	13				11	31	2		
40. *Callista chione* (L.)	2	3			2							2		
41. *Dosinia exoleta* (L.)	14	11	1	2	11						8	2		
42. *D. lupinus* (L.)	53			1	27		12	12	1		4	27	8	10
43. *Venus verrucosa* L.	3	2	1		1					1		1		1
44. *Circomphalus* (*Venus*) *casina* (L.)	29	14	1	12	4	7		3		3	21	2		2
45. *Timoclea* (*Venus*) *ovata* (Pennant)	82	25	2	5	46	11	1	3		14	42	13	6	12

Occurrence by sample, i.e. presence/absence

Species	Live occurrences	Dead occurrences	Allen	Crawshay	Ford	Smith	Holme 1959	Holme 1961, 1966	Probert	This paper	Substrate: Gravel	Sand	Mud	Unassoc'd
46. *Claunirella (Venus) fasciata* (da Costa)	84	24	3	3	22	11	1	3		41	73	1		6
47. *Chamelea (Venus) striatula* (da Costa)	43				43							19	11	10
48. *Paphia (Venerupis) aurea* (Gmelin)	9	10					2	5	2			7	2	
49. *P. rhomboides* (Pennant)	44	25	3	2	17	3	1	2		16	32	1	2	7
50. *Venerupis pullastra* (Montagu)	2				2									2
51. *V. saxatilis* (Fleuriau)	1				1									1
52. *Notirus irus* (L.)		3												
53. *Mysia undata* (Pennant)	6				1		1	4				4	1	1
54. *Lutraria lutraria* (L.)	23				19		1	3			1	10	8	4
55. *L. angustior* Philippi	2	11						1		1	2			
56. *L. magna* (da Costa)	9				9						7	1		1
57. *Gari depressa* (Pennant)	2				2							2		
58. *G. costulata* (Turton)	12		1	3	5	1		2			6	2	3	1
59. *G. fervensis* (Gmelin)	11	3			4		1	4	2			7		
60. *G. tellinella* (Lamark)	39	25			20	2	1	7		9	30	4	1	3
61. *Solecurtus chamasolen* (da Costa)	22				11		5	6			3	3	8	7
62. *S. scopula* (Turton)	6	4			6						4			
63. *Mactra corallina* (L.)	31				28		1	2				21	6	2
64. *Spisula solida* (L.)	50	24		3	24					23	38	2	2	5
65. *S. subtruncata* (da Costa)	22	7			22							8	8	5
66. *Abra prismatica* (Montagu)	36	3		1	23		6	3	3			26	3	6
67. *A. nitida* (Müller)	7				4				3				7	
68. *A. alba* (Wood)	87				71	1	6	3	6		1	32	23	24
69. *Arcopagia crassa* (Pennant)	28	18	1	1	13	2	2	3			6	26		1
70. *Tellina donacina* L.	12	12			4	1	2	4		1	2	4	1	3
71. *T. pygmaea* Lovén	33	15			17	7		2		7	27	1	1	3
72. *T. fabula* Gmelin	15	3			9		1	2	3			9	4	1
73. *T. squalida* Montagu	1							1						
74. *Donax vittatus* (da Costa)	3				3							2		
75. *Phaxas pellucidus* (Pennant)	105				76		12	10	7		3	39	22	29
76. *Ensis ensis* (L.)	29				23		2	2	1	1	4	16	3	4
77. *E. arcuatus* (Jeffreys)	16	2			12		1	1		2	10	2	•	4
78. *E. siliqua* (L.)	4				2			1		1	2	1		1
79. *Hiatella arctica* (L.)	19	9		16	1		2				8	4		
80. *H. striata* (Fleuriau)	9			8	1						2	3		4
81. *Corbula gibba* (Olivi)	46	12			43			3			2	20	13	8
82. *Mya truncata* L.	6				6								3	3
83. *Sphenia binghami* (Turton)		5												
84. *Barnea parva* (Pennant)	1		1								1			
85. *Pholadidea loscombiana* Turton	1		1								1			
86. *Lyonsia norwegica* Macgillivray	4		1		1			2			1	2		
87. *Pandora pinna* (Montagu)	3		1					2				3		
88. *Cochlodesma praetenue* (Montagu)	1		1								1			
89. *Thracia phaseolina* (Lamark)	2							2				1	1	
90. *T. pubescens* (Montagu)	1						1					1		
91. *T. convexa* (Wood)	5				3		2					1	3	1
92. *T. villosiuscula* (Macgillivray)	10	11			3			6			1	6	3	1

GASTROPODA

Species	Live occurrences	Dead occurrences	Allen	Crawshay	Ford	Smith	Holme 1959	Holme 1961, 1966	Probert	This paper	Substrate: Gravel	Sand	Mud	Unassoc'd
93. *Emarginula reticulata* Sowerby	9	13	7	2										7
94. *E. conica* Lamark	1	11	1											1
95. *Diodora apertura* (Montagu)		8												

Species	Live occurrences	Dead occurrences	Allen	Crawshay	Ford	Smith	Holme 1959	Holme 1961, 1966	Probert	This paper	Gravel	Sand	Mud	Unassoc'd
											Substrate			
GASTROPODA (*cont.*):														
96. *Patella intermedia* Jeffreys		2												
97. *Patina pellucida* (L.)	1			1								1		
98. *Acmaea virginia* (Müller)		13												
99. *Calliostoma zizyphinum* (L.)	8	12	3	5							3	1		1
100. *C. papillosum* (da Costa)	7		4	3							1			3
101. *Cantharidus montgui* (Wood)	2			2										
102. *C. striatus* (L.)		2												
103. *Monodonta lineata* (da Costa)		3												
104. *Gibbula magus* (L.)		12												
105. *G. cineria* (L.)		15												
106. *G. umbilicalis* (da Costa)	1	16								1	1			
107. *G. tumida* (Montagu)	1			1										
108. *Tricolia pullus* (L.)		13												
109. *Lacuna pallidula* (da Costa)	1	5								1	1			
110. *Littorina saxatilis* (Olivi)		1												
111. *L. littoralis* (L.)		1												
112. *Alvania crassa* (Kanmacher)		1												
113. *A. punctura* (Montagu)		9												
114. *Rissoa crassa* (da Costa)	1	1			1									1
115. *R. inconspicua* Alder		1												
116. *R. parva* (da Costa)		15												
117. *R. membranacea* (Adams)		10												
118. *Turritella communis* Risso	15	6	2	2	9			2			1	5	2	6
119. *Aporrhais pespelecani* (L.)	3	4	3	3							1		1	1
120. *Bittium reticulatum* (da Costa)		15												
121. *Triphora perversa* (L.)	1	7	1								1			
122. *Clathrus clathrus* (L.)		2												
123. *C. turtonis* (Turton)	1			1										
124. *Eulima glabra* (da Costa)	1						1					1		
125. *Balcis alba* (da Costa)	4	5	2	2							1			2
126. *Lunatia catena* (da Costa)	2	2						2			1	1		
127. *L. alderi* (Forbes)	36	17	1	1	16	2	1	4	2	9	15	12	4	3
128. *L. montagui* (Forbes)	2				2						1	1		
129. *Calyptraea chinensis* (L.)	1	1			1									1
130. *Capulus ungaricus* (L.)	5	2	5								1			4
131. *Erato voluta* (Montagu)		1												
132. *Trivia* sp.	8	8	6	2							1	3		2
133. *Lamellaria perspicua* (L.)	5		3	2							1	3		2
134. *Simnia patula* (Pennant)	8	1	3	5							3	4		
135. *Trophon muricatus* (Montagu)		1												
136. *Ocenebra erinacea* (L.)	1	10												
137. *Colus gracilis* (da Costa)	17		1	16							8			1
138. *Buccinum undatum* L.	1			1							1			
139. *Colus jeffreysianus* (Fischer)	20		12	8							4	5		6
140. *Hinia incrassata* (Ström)	6	14	2	2	2						3	2		
141. *H. reticulatus* (L.)	11	1			7			4			1	7	1	1
142. *Cytharella coarcta* (Forbes)		8												
143. *C. linearis* (Montagu)	1	16		1							1			
144. *Philbertia gracilis* (Montagu)	1	3		1							1			
145. *Acteon tornatilis* (L.)	1				1							1		
146. *Cylichna cylindracea* (Pennant)	15				9		2		4			9	3	3

Species	Live occurrences	Dead occurrences	Allen	Crawshay	Ford	Smith	Holme 1959	Holme 1961, 1966	Probert	This paper	Gravel	Sand	Mud	Unassoc'd
											Substrate			
147. *Scaphander lignarius* (L.)	4						4				1	1	1	
148. *Philine* sp.	12				9		1	2				3	7	1
ECHINODERMATA														
149. *Antedon bifida* (Pennant)	2			2										2
150. *Astropecten irregularis* (Pennant)	26		12	5	1			8			2	13	2	5
151. *Luidia sarsi* Düben and Koren	4		2	2								1		1
152. *L. ciliaris* (Philippi)	15			15							3			
153. *Anseropoda placenta* (Pennant)	13		6	5						2	3	8		1
154. *Porania pulvillus* (Müller)	11		3	8							1	1		2
155. *Solaster papposus* (L.)	25		13	12							4	5		5
156. *Henricia sanguinolenta* (Müller)	11		5	6								5		3
157. *Asterias rubens* L.	49		15	19	3			11		1	10	16	1	5
158. *Marthasterias glacialis* (L.)	27		14	13							6	10		5
159. *Ophiothrix fragilis* (Abildgaard)	48		16	13	10	1	5	3			10	19	1	9
160. *Ophiocomina nigra* (Abildgaard)	83		9	63	2			9			29	9		10
161. *Ophiactis balli* (Thompson)	44		11	32	1						13	5		7
162. *Amphiura chiajei* Forbes	1							1			1			
163. *A. securigera* (Düben and Koren)	2							2			1	1		
164. *A. filiformis* (Müller)	47		1		27		5	7	7		3	23	9	8
165. *Acrocnida brachiata* (Montagu)	7				1		2	4				5	1	
166. *Amphipholis squamata* (Delle Chiaje)	1						1							1
167. *Ophiura texturata* Lamark	69		14	12	25	4		9	5		14	31	7	11
168. *O. albida* Forbes	34		10	15				6	3		12	7	3	4
169. *O. affinis* Lütken	17		1	2		1	10	2	1		3	10	1	1
170. *Psammechinus miliaris* (Gmelin)	17		13	2	1			1			4	6		5
171. *Echinus esculentus* L.	39		12	26	1						10	6		7
172. *E. acutus* Lamark	16		7	9							2	3		4
173. *Echinocyamus pusillus* (Müller)	90	25	7	4	31	21	6	4		17	57	13	1	13
174. *Spatangus purpureus* (Müller)	30		7	14	4	1		1		3	16	3		4
175. *Echinocardium cordatum* (Pennant)	61		2		37		10	8	4		1	33	10	14
176. *E. flavescens* (Müller)	5				4	1					4			1
177. *E. pennatifidum* (Norman)	2		1	1							2			
178. *Holothuria forskali* Delle Chiaje	1							1					1	
179. *Cucumaria elongata* Düben and Koren	30				22	1	3	5			3	8	11	6
180. *C. hyndmani* Thompson	1			1										
181. *C. lactea* (Forbes)	6		6								3	3		
182. *Thyone fusus* (Müller)	10		1	2	2		1	4			3	1		4
183. *T. raphanus* Düben and Koren	2			1			1				1		1	
184. *Pseudocucumis mixta* Östergren	3							3			3			
186. {*Leptosynapta inhaerens* (Müller) / *Labidoplax digitata* (Montagu)	31				12		11	8			1	15	10	4

APPENDIX 2

Details of locations of stations (text-fig. 2) as Decca positions (as read) and transits.

Author's station number	Depth	Red	Green	Purple	Direction of towing
Eddystone: Allen (1899)					
55	64 m	A 11·7	D 33·0	A 74·4	A 11·7
87	60 m	A 10·5	D 30·6	A 74·65	A 10·5
88	60 m	A 11·7	D 30·5	A 72·7	Eastwards
89	60 m	A 10·0	D 31·5	A 76·0	A 10·0
Stoke Point					
1	32 m		D 33·8	A 72·2	Line up gun and point
2	35½ m		D 33·8	A 72·2	Stoke Campsite just open
3	23½ m		D 32·0	A 70·3	All towing to land

Author's station number	Depth	Transits	Direction of towing
Plymouth Sound Ford (1923)			
23	14 m	Duke Rock buoy on Bovisand Point Western Breakwater Lighthouse on New Gravel buoy	Towards Plymouth
47	15 m	Mewstone on 4th blockhouse from lighthouse western end of breakwater Left-hand victualling yard chimney on Barn Point light beacon	Towards Plymouth
90	14 m	New Ground buoy under inner end of Batten Breakwater Top of Mewstone on 2nd block-house west end of breakwater	Towards Plymouth
Qu 3	15 m	Line buoy with left-hand side of Fort Tall flats on east end of Drakes Island.	Towards Plymouth